Skipping swans

Beekman, J.H.; Nolet, B.A.; Klaassen, M.

SKIPPING SWANS: FUELLING RATES AND WIND CONDITIONS DETERMINE DIFFERENTIAL USE OF MIGRATORY STOPOVER SITES OF BEWICK'S SWANS *CYGNUS BEWICKII*

JAN H. BEEKMAN [1,2], BART A. NOLET [1] & MARCEL KLAASSEN [1]

Some migratory birds refuel at stopover sites that they by-pass on the return trip. In theory, this skipping behaviour is only expected in time-selected migrants when the overflown site is of a lower quality than the departure site. We provide empirical evidence that quality differences in stopover sites are the cause for skipping in Bewick's Swans *Cygnus bewickii* tracked by satellite telemetry. Two and five complete tracks were recorded in spring and autumn, respectively, showing that the White Sea was visited for *c.* 2 weeks in spring, but by-passed (or visited for a few days at the most) in autumn. Skipping of the White Sea in autumn was predicted by a dynamic programming model which was based on calculated gain rates during stopover in the Pechora Delta and the White Sea. This prediction was not sensitive to plausible variations in gain rates. Relative to the Pechora Delta the White Sea is a poor site because a large tidal amplitude precludes foraging on the beds of the submerged macrophyte Fennel Pondweed *Potamogeton pectinatus* during high tide. The dynamic programming model predicted a fast autumn migration. However, the phenology of autumn arrival dates of Bewick's Swans on the wintering grounds revealed that only in three out of ten years a significant number of birds was able to reach the wintering grounds without refuelling. In the other years, unfavourable wind conditions along the Russian/Baltic part of the route prevented such non-stop migration.

Key-words: *Cygnus bewickii* – fuelling rates – dynamic programming – optimal migration – satellite tracking – wind assistance.

[1]Centre for Limnology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 1299, NL-3600 BG Maarssen, The Netherlands, E-mail: b.nolet@nioo.knaw.nl; [2]Zoological Laboratory, University of Groningen, P.O. Box 14, NL-9750 AA Haren, The Netherlands
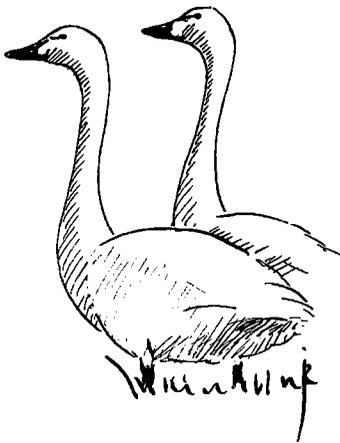
INTRODUCTION

Migratory birds travel between their summer and winter range twice a year. In spring and autumn they face different environmental conditions. These may result in different migration strategies. In order to maximize fitness, migrants have to make a number of decisions related to the speed at which to migrate or the amount of fuel to deposit. In small passerines, migration speeds are higher in spring than in autumn, which has been attributed to the importance of being as early as possible on the breeding grounds (Fransson 1995). However, whether such seasonal differences in migration speed apply may depend on body size and foraging ecology. In terrestrial grazing waterfowl, for

example, the speed of migration may be limited by the timing of snowmelt and plant production along a latitudinal gradient. Indeed, it has been suggested that the migration of herbivorous waterfowl is tuned to developments in plant quality and production (Drent *et al.* 1978). Likewise, in spring, the speed of migration of aquatic foraging birds might be limited by the sequence of ice break-up along the migratory route. In autumn, date and sequence of freeze-up of stop-over sites may dictate the timing of departure and the speed of migration.

Large birds are confronted with lower maximum fuel deposition rates (percentage of daily mass increase relative to lean body mass), because the maximum limit of the daily metabolisable energy intake is proportional to basal metabolic rate rather than to body mass (Lindström 1991). Thus, large, long-distance migratory birds that use costly flapping flight (Norberg 1996) need multiple stopover sites *en route* where they stage for relatively long periods to refill their fuel stores (Hedenström & Alerstam 1997). Suitable feeding habitats are often discretely distributed and far apart, separated from each other by unsuitable habitat ('ecological barriers'), such as seas, deserts or frozen taiga zones (Alerstam 1990). In such cases, the birds can only refuel at certain stop-over sites, and are forced to follow a so-called 'stepping-stone' migration strategy. This may occur in different forms (hop, skip or jump; Piersma 1987). With an increase in fuel load the flight energy costs per unit distance increase. In order to minimise transport costs a migratory bird should travel as light as possible. Thus, from an energetic point of view the best strategy would be to use all potential refuelling sites along a migratory route ('hopping'). If, however, the bird tries to minimise time rather than energy, it could be better to put on larger fuel loads at high quality stopover sites (Alerstam & Lindström 1990). Under some circumstances, for time-constrained migrants it may even be optimal to by-pass a stopover site of relatively poor quality ('skipping'). Skipping should occur when the next stop-over site in line (i.e., the first stop-over site after the skipped site)

can be reached more quickly by a non-stop flight by putting on enough weight at the departure site (Gudmundsson *et al.* 1991). Several patterns of bird migration have been described suggesting that skipping is a rather general phenomenon, especially in waders and geese breeding in the High Arctic. In spring, waders congregate at a few sites, whereas in autumn they are much more widespread (Gudmundsson *et al.* 1991). In autumn, Barnacle Geese *Branta leucopsis* and Pink-footed Geese *Anser brachyrhynchus* nesting on Spitsbergen and wintering in Scotland and along the east coast of the North Sea respectively, completely overfly one stop-over site in Norway which is always visited in spring (Madsen *et al.* 1999). However, the link with the quality of fuelling sites is unclear and hence the cause for this migratory behaviour.

This paper describes seasonal differences in migration patterns of Bewick's Swans *Cygnus bewickii*. We tracked Bewick's Swans by satellite in both spring and autumn and noted that the swans skipped the White Sea as stop-over site in autumn whereas it was extensively used in spring. In addition, we collected data on food intake rates at different stop-over sites. We then used dynamic programming (Mangel & Clark 1988; Weber *et al.* 1998) to investigate whether the measured differences in refuelling rates could explain the observed skipping behaviour. This is the first study that models skipping behaviour using empirical fuelling rates. The model is further used to identify crucial factors determining the migratory behaviour of the swans. In order to explain deviations from the dynamic programming model, we used wind data along the migratory route to analyse the timing of departure of satellite birds from stop-over sites in autumn 1998, and we compared phenological data on arrival to The Netherlands with prevailing wind conditions en route from a ten-year period to explain inter-annual variation in autumn arrival dates.
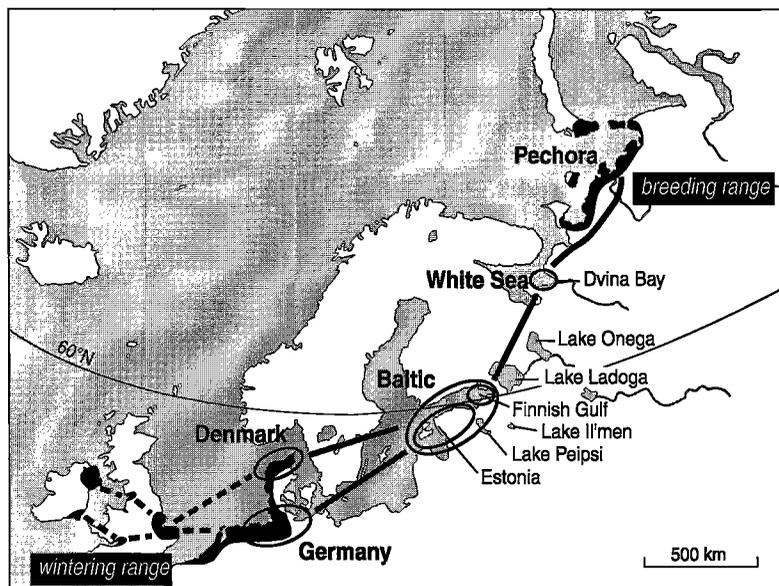
Fig. 1.   Winter and summer distribution of the NW-European flyway-population of Bewick's Swans, with migratory route and main stopover sites indicated. Names of locations in eastern Europe that are mentioned in the text are also indicated.

STUDY SYSTEM

Bewick's Swans are long-distance migrants that breed and moult in northern Russia in summer and spend the winter in Western Europe (Fig.1). Twice a year they migrate the 3000-4000 km that separate their summer and winter ranges. Fitness consequences of migratory behavioural decisions by these large bodied arctic breeding waterfowl are constrained by the fact that their short reproductive season in the subarctic has a small safety window for successfully rearing offspring (Rees *et al.* 1997). The breeding cycle of Bewick's Swans (from acquiring a territory to fledging cygnets) lasts about 110 d, whereas the frost-free period in the Pechora Delta is about 120 d (Jun-Sep). Cygnets that have not fledged before October 1 risk a total freeze-over of tundra lakes, which denies them access to food. These late cygnets usually die during an early onset of winter (pers. obs.), analogous to conditions faced by Tundra Swans in Alaska (J. Helmericks pers.

comm.). Birds must therefore arrive in time on the breeding grounds. The maximum flight distance that Bewick's Swans can cover without refuelling is about 2000 km (see Appendix and Table 1 for details). Hence, the swans need at least one stopover site where they can refuel to complete each journey. Important stopover sites are situated in northern Germany (8000 birds) and northern Denmark (3500 birds), in the Baltic region (20 000 birds) and in the White Sea in Russia (up to 18 000 birds), while a large pre-migratory gathering (5000-15 000 birds) is found in the Pechora Delta in autumn (Fig.1, see also Rees *et al.* 1997). There is a striking difference in the duration of the migratory period. Based on peak departure and arrival dates of the population as a whole, spring migration takes three months and autumn migration one month and a half. This seasonal difference in speed of migration suggests that the swans either have different goals in spring and autumn or that they face different conditions en route.

Bewick's Swans rely almost entirely on sub-

Table 1. Characteristics of the Bewick's Swan used in the dynamic programme. [a]of lean body mass; [b]calculated using average body mass (7.00+7.00/1.24)/2=6.32 kg; [c]assuming 50% resting of total time; [d]assuming a ground speed of 72 km h^{-1}

Parameter	Value	Unit	Reference
Top-up mass	7.00	kg	
Maximum fuel load	24	%[a]	Hedenström & Alerstam (1992)
Energy density of fuel stores	30	MJ kg^{-1}	Klaassen (1996)
Maximum fuel store (x_{max})	40.5	MJ	30×0.24/1.24x7.00
Daily energy expenditure (E)	2.4[b]	MJ day^{-1}	Bruinzeel et al. (1997)
Wing span	2.05	m	
Aspect ratio	8.67		
Body drag coefficient	0.1		Pennycuick et al. (1996b)
Air speed	64	km h^{-1}	This study
Migration speed (v)	864[c,d]	km day^{-1}	
Maximum range (D_{max})	2023[d]	km	

merged macrophytes as a food resource at migratory sites, especially north of 60°N (Beekman *et al.* 1996b). The swans especially prefer the tubers of Fennel Pondweed *Potamogeton pectinatus* (Nolet *et al.* 2002). Ice cover may prevent swans to access this aquatic food source. The swans dig pits with their feet to reach the tubers (Brouwer & Tinbergen 1939; Van Eerden *et al.* 1997). Tuber densities can be measured before and after swan grazing, and site-specific intake rates can therefore be assessed (e.g., Beekman *et al.* 1991). The birds deplete the tubers to a level that under most circumstances guarantees a complete recovery of the tuber bank in the next autumn (Van Vierssen *et al.* 1994). South of 60° latitude, grassland and arable land with crops and harvest left-overs are also used as feeding habitats, particularly in spring (Dirksen *et al.* 1991; Degen *et al.* 1996; Laubek 1995).

METHODS

In order to track the spring migration, three Bewick's Swan males were caught by canon-net in Kaansoo in Estonia (58°36'N 25°08'E) on 10 April 1993 and another ten in Vendsyssel, Northern Jutland, in Denmark (57°09'N 09°51'E)

between 26 March and 1 April 1996. These birds were equipped with 90-95 g PTT-100 transmitters (Microwave Telemetry) and neck-collars. In 1993, the transmitters were only glued onto the back feathers, and transmission was 12 h on: 12 h off in the one successfully tracked bird (#14551, blue neck-collar 902U). In 1996, a neoprene harness was used in addition (Pennycuick *et al.* 1996a), and transmission was continuous (bird #16109, blue neck-collar 110U).

In autumn, five male swans were caught between 13 and 15 August 1998 in the Pechora Bay in northern Russia: three (#7274, #7275 with blue neck-collar and #7292) along the northern shore of the Korovina Bay (Korovinskaya Guba) between 68°20'N 53°49'E and 68°22'N 53°38'E and two in a small moulting flock of 30 birds north of Zelonii Ostrov (68°20'N 54°12'E). The birds were flightless due to wing moult and were easily caught with a small boat using a hook. The swans #7274 and #7275 were paired with unmarked females, and swan #7292 was unpaired. None of the satellite birds was accompanied by cygnets. We glued 45 g PTT-100 transmitters (Microwave Telemetry) onto the back feathers and attached it further with a harness of knicker-elastic (Glahder *et al.* 1998). Transmission was set at 12 h on / 78 h off during the first

month and subsequently at 12 h on / 30 h off.

The signals of the transmitters were picked up by two nominal and two support NOAA series satellites, and sent to the Argos operator CLS in Toulouse, France. In 1993, only two nominal satellites were operational and data were received as hardcopies. In 1996 and 1998 we collected our data by an on-line connection with CLS (see Pennycuick *et al.* 1996a). The data consisted of the transmitter identification, date, time, a location and an alternative location, and a measure of the accuracy (0: >1 km; 1: 1000-350 m; 2: 350-150 m; 3: < 150 min; in 1993, class 0 indicated an accuracy of > 1 km if PTT contact was > 200 s, and no accuracy if pass duration was shorter; in later years, accuracy was further classified as Z: rejected; B and A: no accuracy). Because the transmitters used for tracking the autumn migration were not continuously sending, in most cases we only had a good measurement of either the time of departure or the time of arrival. We therefore calculated the flight time (the great circle distance divided by the ground speed of the birds) in order to estimate the moment of departure or arrival (whichever was missing) or both (by assuming that the flight occurred midway between the last location at the departure and the first location at the destination site). When no more accurate fixes were available, fixes with an accuracy measure of 0, A or B were averaged when close to each other in space and time. If the calculated flight time was greater than the time elapsed between two consecutive fixes, we tried whether the alternative location gave a smaller discrepancy, and chose the alternative when it did. The overall wind assistance (see below) over a trajectory consisting of more than one flight was weighted by the individual flight times. The flight time multiplied by the fixed air speed gives the air distance. The ground distance over a trajectory is the sum of the great circle distances. The speed of migration, i.e. the great circle distance divided by flight time plus stop-over time, was calculated using stopover duration prior to leaps in spring and using stop-over duration after leaps in autumn.

Wind assistance

We calculated the ground speed (V_g) and the wind assistance (V_{tw}) of the satellite birds by combining a fixed air speed (V_a) and the local wind speed (V_w, obtained from maps of the Deutsche Wetterdienst) following Piersma & Jukema (1990), using the rhumb line direction between fixes as the bird's heading. We calibrated V_a from a series of three high quality (category 1) fixes four hours apart during the long-distance departure flight of swan #7274 from the Pechora Delta to the Mezen Bay on 25 September 1998 (Fig. 3b) when it had a tailwind vector ($V_{tw} = V_g - V_a$) of 8.3-8.9 km h^{-1}, giving a V_a of 64 km h^{-1}.

During 1990-99, we counted Bewick's Swans in Lauwersmeer, The Netherlands, at intervals of 1-3 d from the moment the very first birds were seen or reported. Lauwersmeer is the first site to be visited by Bewick's Swans in The Netherlands in autumn. We defined first arrival date as the day on which at least 400 birds were counted simultaneously on the lake. In order to analyse the potential effect of wind assistance along the flyway on these first arriving swans, we collected data on wind speed and wind direction from maps of the Deutsche Wetterdienst at five locations with weather stations, i.e. Pechora Delta (Nar'yan Mar), White Sea (Archangelsk), Finnish Gulf (St. Petersburg), Baltic coast (Kaliningrad) and The Netherlands (Eelde). Because departure from the Pechora Delta normally commences in the last week of September, we analysed wind data from the period 23 September to 7 October for each year and each station. Wind assistance at each station was calculated using the same method as for the satellite birds.

Dynamic programming

Dynamic programming (Mangel & Clark 1988) was used to be able to compare the observed migration schedules with those predicted for a hypothetical Bewick's Swan maximising its fitness. Both the spring and autumn migration were modelled. We used a toolbox (Klaassen 2001) that largely follows the concept presented by Weber *et al.* (1998). Five potential staging sites *i* were dis-

tinguished: the wintering site (The Netherlands), three stop-over sites (the Elbe region in Germany, Estonia and the Finnish Gulf in the Baltic region, and the Dvina Bay of the White Sea in Russia) and the breeding site (the Pechora Delta in Russia). The distances D_i between these sites are 400, 1000, 1100, and 750 km. The migration period was divided into whole days t. Fitness reward in spring was expressed as the probability of successful breeding, whereas in autumn it was expressed as survival probability. Preparations for spring migration were assumed to start on 16 February (day 47) and the arrival date to achieve maximal fitness was set at 28 May (day 148). Arrival at the breeding grounds on any other day led to complete breeding failure. The latter assumption was justified for in this large bird species the time window for successful breeding is extremely narrow (Rees *et al.* 1997). In addition, the increase in population numbers over recent decades (Rees *et al.* 1997) has intensified competiton for breeding sites, which in theory leads to a highly synchronised arrival at an early date (Kokko 1999). For autumn migration, preparations were assumed to start at 1 September (day 244). Optimal date of arrival at the wintering grounds was also set at the first of September, the expected fitness gradually decreasing after this date, reaching 0 by the last day of the year.

Given the temporal and spatial variation in food availability (see below), we used the dynamic programme to determine the optimal behavioural decisions for an average male Bewick's Swan (Table 1) as a function of its fuel stores, time of year and staging site. At time point t, the expected future fitness F is a function of the swan's fuel stores x, and its location i: $F(x,t,i)$. The variable x varies between 0, where the swan dies of starvation and x_{max}, where it has reached its maximum fuel load. At the destination site N, the expected future fitness is $F(x,t,N)$ (Appendix 1). At each time point when the swan has not yet arrived at its destination it has two behavioural options: either foraging at intensity u ($0 \le u \le 1$) or, if fuel stores permit, flying to one of the next sites. The optimal behavioural decisions for all combinations of fuel

stores, time and site are determined by backward calculations. This results in a decision matrix that is subsequently used by our virtual swan on its migratory journey. These forward simulations yield a prediction of the timing and intensity of use of the various sites along the migration route. The conditions in which skipping of the White Sea stopover site occurred were investigated by concurrently varying the quality of the preceding site (the Baltics in spring and the Pechora Delta in autumn) and the quality of the White Sea site itself.

Empirical data input

The daily time spent foraging by the swans was determined by scan sampling (Altmann 1974), and was multiplied by the rate of metabolizable energy intake while foraging (*mei*) to obtain the daily *MEI* at each staging site. For Bewick's Swans on migration these daily intake rates probably represent maximum intake rates constrained by foraging time (B.A. Nolet & M. Klaassen, unpubl.). In spring, Bewick's Swans feed on grass in both The Netherlands and Germany (Rees *et al.* 1997). At more northerly stopover sites, the main food is submerged macrophytes, in particular tubers of Fennel Pondweed, in both spring and autumn (Estonia: Luigujõe *et al.* 1996; White Sea: Nolet *et al.* 2001a; Pechora Bay: M. Klaassen, T. de Boer & H. Hangelbroek, unpubl. data). In the dynamic programming model, the decisions of the modelled swan are independent of those of other swans. There are however clear indications from field observations that depletion of fuelling resources plays an important role and will select for early migration (Nolet & Drent 1998). We therefore implicitly included this social aspect in the model by postulating a reduction in daily *MEI* due to depletion.

For swans feeding on grass in spring, scans were made in the Onnerpolder near Haren in The Netherlands and in the Börmer- and Meggerkoog near Bergenhusen in Germany in 1994 (J. Nienhuis & M. Epe, unpubl. data). In this case, *mei* was calculated from dropping intervals, dropping weights, and chemical analyses of energy content

and cell wall components of food and droppings. This method is described in more detail by Prop & Vulink (1992). However, acid detergent fiber was used as an internal marker instead of lignin to estimate the digestibility of the food and energy as the food component of interest. In the Baltic and the White Sea, ice cover prevented sampling a large enough area of the pondweed bed before the swan grazing in spring. At these stop-over sites we estimated the swans' daily time spent foraging by scan sampling in spring 1996 (J. Nienhuis, unpubl. data; Nolet & Drent 1998). In the White Sea, the proportion of the day spent foraging decreased linearly with date during the stopover period due to food depletion (Nolet & Drent 1998). Such data are lacking for the Baltic, but tentatively we assumed that the proportional rate of food depletion was the same for the Baltic and White Sea. Bruinzeel *et al.* (1997) provide an allometric equation for *mei* (in W) for tuber-eating waterfowl species: $mei = 29.5 \, M^{0.86}$, where M is body mass in kg. The daily *MEI* was obtained by multiplying this figure for a typical Bewick's Swan with the observed proportion of the day spent foraging (Table 2).

In autumn, we measured the tuber biomass both before and after swan grazing as well as the intervening swan exploitation in the Pechora Delta and in The Netherlands. In the Pechora Delta, these data were gathered at a pondweed bed of 6.3 ha in September 1998. Fresh weight were converted to dry weights using the measured tuber dry weight percentage of 23.8%. For the Pechora we assumed that no tuber depletion occurred, because of the extensiveness of vegetation beds (2250-4500 ha, Beekman *et al.* 1996b) and because tubers were still being formed during the period of swan grazing (M. Klaassen, T. de Boer & H. Hangelbroek, unpubl. data). In The Netherlands, the same kind of data were obtained at a pondweed bed of 10.4 ha in September-November 1995 and 1996 (Nolet *et al.* 2001c). Here all collected tubers were dried to constant weight. The gross food intake per foraging swan was converted to *mei* using a tuber energy content of 17 kJ g^{-1} dry weight (Beekman *et al.* 1991) and a metabolisability of tubers of 90% (Nolet *et al.* 1998). For the White Sea and the Baltic we assumed the same maximum *MEI* in autumn as in spring, because no production of tubers occurs in winter.

Table 2. Site-specific daily metabolisable energy intake rates of Bewick's Swans during spring and autumn migration. [a]at the plateau level in Fig. 2; [b]due to increase in daylength; [c]same proportional decrease as in the White Sea; [d]due to depletion; [e]according to Bruinzeel *et al.* (1997); [f]same as spring before depletion; [g]data collected in The Netherlands.

Staging site	Main food	Foraging[a] (h d^{-1})	Δ Foraging (h d^{-1})	*mei* (W)	*MEI*[a] (MJ d^{-1})	Reference
Spring						
Netherlands	Grass	5.6	+0.15[b]	105	3.4	1
Germany	Grass	10.8	+0.16[b]	90	3.6	1
Estonia	Tubers	18.7	-0.81[c,d]	144[e]	9.7	1
White Sea	Tubers	11.5	-0.50[d]	144[e]	6.0	2
Autumn						
Pechora Delta	Tubers	20.4		162	11.9	3
White Sea	Tubers				6.0[f]	
Estonia	Tubers				9.7[f]	
Germany[g]	Tubers	13.7		146	7.2	4

References: (1) J. Nienhuis (unpubl. data), (2) Nolet & Drent (1998), (3) M. Klaassen, T. de Boer & H. Hangelbroek (unpubl. data), (4) Nolet *et al.* (2001c)
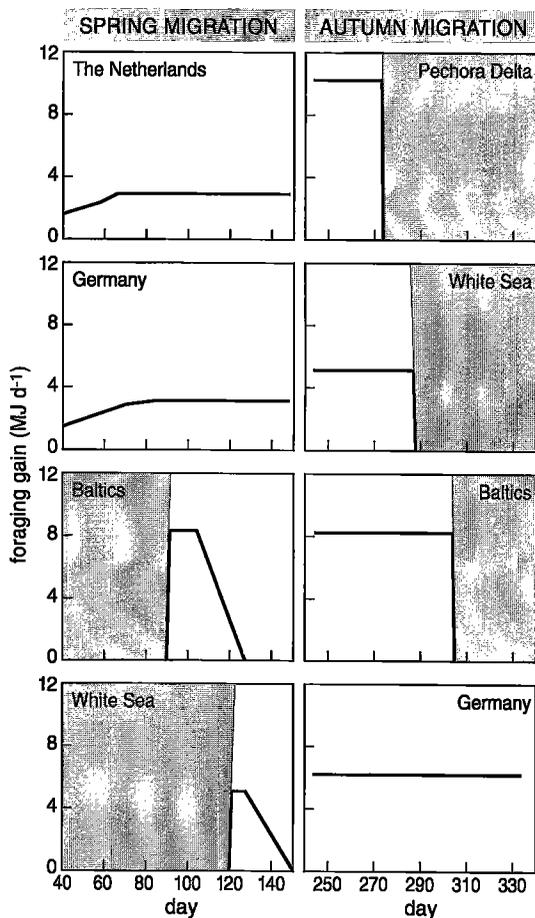
Fig. 2. Calculated daily foraging gains G for each stop-over site in spring and autumn. In spring, terrestrial food plants are eaten in The Netherlands and Germany, whereas submerged macrophytes form the diet in Estonia and White Sea. In autumn, submerged macrophytes are eaten at all four stop-over sites. Periods with ice cover are shaded. Spring foraging gains for Bewick's Swans in The Netherlands and Germany are based on data gathered on Bewick's Swans foraging on grass by J. Nienhuis (unpublished data). Ice break-up in Estonia and White Sea is estimated to take place at the 4th and 14th of April respectively. Foraging gains are based on a predicted net intake rate of 0.5 MJ h^{-1} of foraging for our model swan (Table 1) (Bruinzeel *et al.* 1997) and the observed foraging activity of Bewick's Swans in Estonia (J. Nienhuis, unpublished data) and White Sea (Nolet & Drent 1998). Data on depletion are not available for Estonia but were taken to resemble depletion in the White Sea. For the autumn situation no depletion is considered. For Bewick's Swan the freezing in while on migration presumably has a high fitness costs. Therefore relatively early dates were taken for the closing of the foraging sites due to ice cover: the 1st of October for the Pechora Delta, the 15th of October for the White Sea and the 1st of November for Estonia. Foraging gains for Pechora Delta are from M. Klaassen, T. de Boer and H. Hangelbroek (unpubl. data), those for White Sea and Estonia are set to the maximum estimates for spring (see above), while those for Germany are based on average intake rates of Bewick's Swans on Fennel Pondweed tubers during autumn in The Netherlands (Nolet *et al.* 2001c). The depicted G values are maximum values reached when the birds feed at intensity $u = 1$.

For the autumn stopover in Germany, we assumed a *MEI* equal to the average *MEI* derived for The Netherlands (Table 2).

Bruinzeel *et al.* (1997) compiled data on daily energy expenditure of herbivorous birds. The majority of these birds were caged, and we regressed cage metabolism (*CMR* in W) against body mass (kg) yielding $CMR = 7.95 \, M^{0.58}$ ($r^2 = 0.91$; $N = 11$; M ranging from 0.34 to 4.5 kg). This is equivalent to 1.7 times basal metabolic rate, and we took this figure as the daily energy expenditure at all sites not taking foraging costs into account (E, 2.4 MJ day^{-1}). Extra foraging time

and heat increment of feeding will increase the energy expenditure of free-living birds. We incorporated these extra costs by multiplying *MEI* by k, the efficiency of utilisation of metabolisable energy for birds feeding on carbohydrates (Blaxter 1989) to obtain the daily foraging gain (G, MJ day^{-1}). k ranged from 0.95 at low intake levels (in The Netherlands and Germany in spring) to 0.8 at high intake levels (in the Pechora Delta in autumn), being 0.85 at intermediate values (in all other cases). For the various sites G varies with time of the year due to ice conditions and depletion (Fig. 2).

RESULTS

Two of the swans followed during *spring migration* were tracked all the way to the breeding grounds, one in 1993 (swan #14551) and one in 1996 (swan #16109) (Fig. 3a). The bird tracked in 1993 was caught during its stopover in Estonia and thereafter made three stopovers before reaching its destination: near Seskar Island in the Finnish Gulf, at Lake Onega near Petrozavodsk, and in the Dvina Bay (White Sea) (Beekman *et al.* 1996a). The second swan had two main stopovers after its departure from Denmark: one in Estonia and one in the Dvina Bay (White Sea). At both sites it was seen while foraging on pondweed tubers. Stopover periods ranged from 12-30 d, averaging 18 ± 7 d. Both birds used the Dvina Bay in the White Sea as a last stopover (17 and 13 d respectively) before departure to the breeding grounds. Ground distances between stopover sites averaged 624 ± 305 km (maximum 1,166 km), which were covered in one to four d (Table 3). The different leaps were usually flown in still to calm air (0 - 2.4 km h^{-1}). Air distances covered were therefore usually only up to 5% shorter than the ground distances. Only during one short leap (256 km) from Estonia to the Finnish Gulf, a wind assistance of 8.6 km h^{-1} resulted in a 12% reduction in the distance actually flown. Non-stop flown distances averaged 350 ± 166 km (maximum 571 km). However, if short stop-overs of up to two d are included (considered to be too short to substantially replenish body stores), the distances covered were much longer and averaged 608 ± 305 km (maximum 1,148 km) air distance. Although these two birds migrated mostly under quiet wind conditions, we have shown elsewhere that wind assistance functions as a trigger for spring migration between the Finnish Gulf and the White Sea (Klaassen *et al.* unpubl. data, Nolet *et al.* 2001a) for the Bewick's Swan population as a whole.

The five swans followed in *autumn* were all tracked along the entire migration route from the breeding grounds to the wintering grounds in The Netherlands (Fig. 3b). All the birds had long non-stop flights following their departure from the Pechora Bay, averaging 1032 ± 363 km; especially the last bird which presumably flew directly from the Pechora Bay to Lake Peipsi on the border between Estonia and Russia (an air distance of 1572 km; Table 3). Three satellite birds made short stops in the White Sea (swan #7275 for 0.4 d in the Onega Bay; swans #7292 and #7293 for 1.9 and 2.3 d, respectively, in the Dvina Bay). However, all these autumn stops were again considered to be too short to substantially replenish body reserves. In fact, all five birds reached the Baltic States within a week after their departure from the Pechora Bay, which represents a ground distance of about 2000 km. They covered average air distances of 2023 ± 192 km (maximum 2322 km) in this period without making stops of more than 2.5 d on their way (Table 3).

Effect of wind on speed of migration

A small part of the population was able to maintain this speed of migration and about 1600 birds arrived to Lauwersmeer in The Netherlands on 2 Oct 1998. This was a very early date for so many Bewick's Swans to reach the wintering-range, since peak arrival in Lauwersmeer usually takes place in the second half of Oct (Table 4). In contrast, the satellite swans staged rather long in the Baltic area (22-45 d, average 32 ± 8 d). Three swans staged in Estonia (swan #7275: Lao-liu coast, Vilsandi and Saaremaa; swan #7293: Peipsi and Pärnu; swan #7273: Pärnu and Matsalu) and the other two swans staged in Lithuania and Kaliningrad (swan #7274: Prienu, Marijampolés and Alytaus; swan #7292: Nemunas river) (Fig. 3b). Water levels in large lakes further to the east in Estonia and western Russia were raised by 1-2 m (L. Luigujõe, V.A. Buzun & J.H. Beekman, unpubl. data), preventing birds to reach food plants in usually shallow parts of these lakes. Consequently, only some hundreds of Bewick's Swans were observed in the Finnish Gulf and in Lakes Ladoga, I'lmen and Peipsi during surveys from aeroplane and boat in peak migration time (16-22 October 1998, J.H. Beekman, unpubl. data).
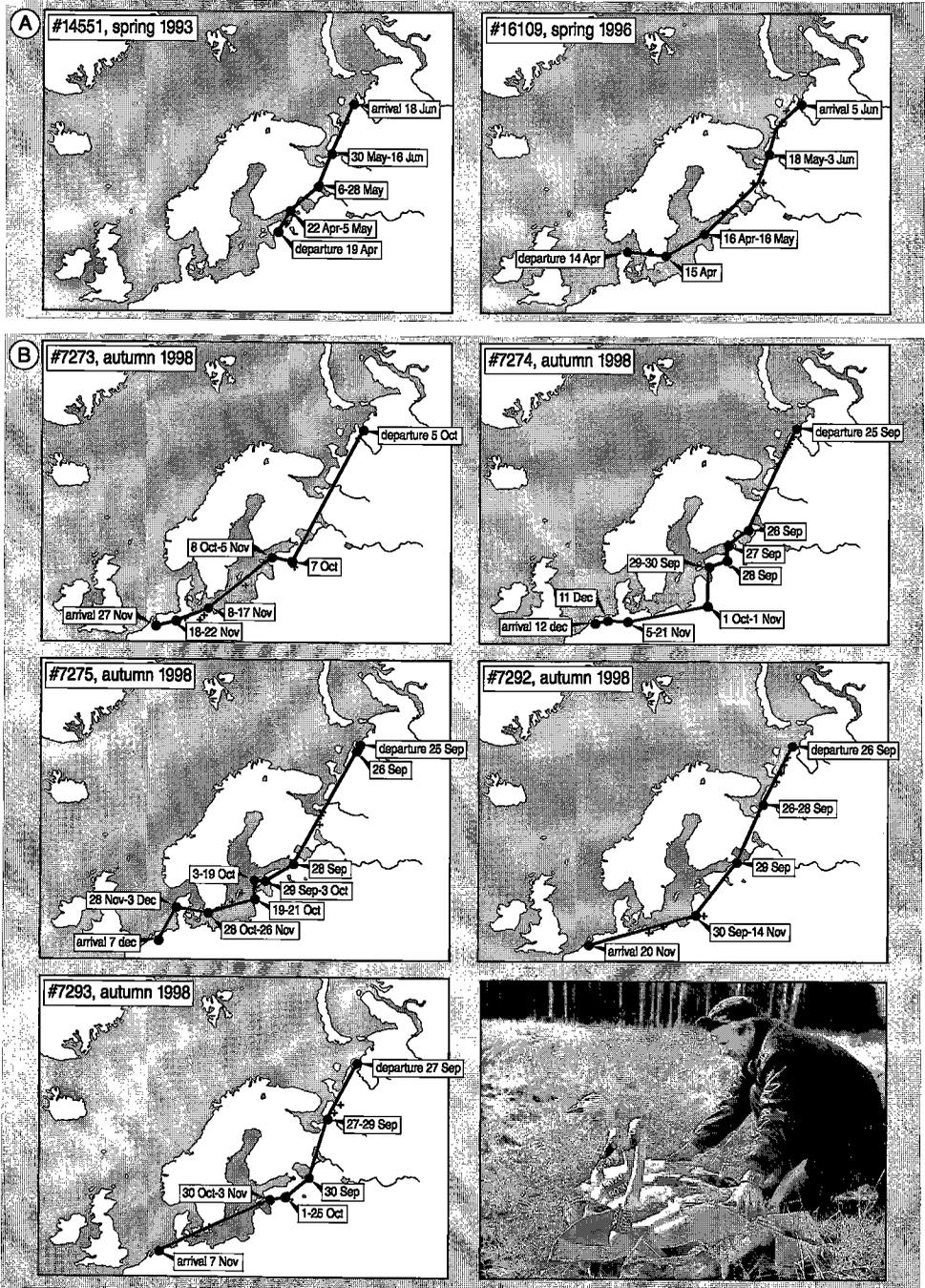
Fig. 3. Migration routes of Bewick's Swans as tracked by satellite in (a) spring 1993 and 1996 and (b) autumn 1998. • indicates stop-over, + indicates flight. The maps have an orthographic projection. The photo shows Dr. Jüri Keskpaik with three satellite birds captured in Estonia, 12 April 1992.

Table 3. Summary of flight performance of Bewick's Swans tracked by satellite over the trajectory Baltics to the breeding grounds in subarctic Russia in spring 1993 and 1996 and autumn 1998. Arrival (on the breeding grounds in spring and in The Netherlands in autumn) is also given. [a]where the bird stopped ≥ 3 d; [b]weighted average during flights.

Swan	Departure	Stopover site[a]	Travel time (d)	Flight time (h)	Wind assistence[b] (km h^{-1})	Air distance (km)	Ground distance (km)	Maximum non-stop flight (air km)	Staging period (d)	Arrival
Spring										
14551	19 Apr	Seskar Island, Finnish Gulf, Russia	3	3.5	8.6	226	256	119	12	
	5 May	Lake Onega, Russia	1	8.5	0.0	543	547	459	20	
	28 May	Dvina Delta, White Sea, Russia	2	7.5	0.0	478	478	368	17	
	16 Jun	Velt' River, Malozemels'kaya Tundra, Russia	3	8.9	1.5	568	581	200	-	18 Jun
16109	16 May	Dvina Delta, White Sea, Russia	4	17.9	1.0	1148	1166	571	13	
	3 Jun	Pechora River, Malozemels'kaya Tundra, Russia	3	10.9	2.4	688	714	383	-	5 Jun
Autumn										
7274	25 Sep	Lithuania	7	36	-0.2	2328	2322	1216	31	12 Dec
7275	25 Sep	Estonia	4	32	-4.7	2014	1868	887	22	7 Dec
7292	26 Sep	Kaliningrad and Lithuania	4	3	3.0	2052	2147	664	45	20 Nov
7293	27 Sep	Estonia	5	29	0.3	1844	1851	821	33	7 Nov
7273	5 Oct	Estonia	3	29	0.9	1875	1903	1572	29	27 Nov

In addition to the adverse feeding conditions further east, strong headwinds in the Baltic region and western Europe throughout October prevented these birds to proceed on their autumn migra-

tion from the Baltic (Fig. 4). Swans #7274, #7275, #7292 and #7293 departed from the Pechora Delta on 25-27 September under favourable tailwind conditions, which was preceded by a three day period of headwinds (see Fig. 4, upper panel). Exactly in this period, mass departure from the Pechora Delta was observed (M. Klaassen unpubl. data). Swan #7273 apparently was not ready to profit from these conditions and had to sit out another 8 d of headwinds until 5 October before the wind again turned to northeast. Swans # 7274 and #7275 passed the White Sea under quiet conditions, swans #7292 and #7293 reached the White Sea slightly later and met a headwind for two d (Fig. 4, second panel from top). This probably explains why these birds made a short stop in the White Sea. After reaching Estonia, none of the satellite birds continued their migration but instead staged in the Baltic region for a considerable period. Apart from difficult access to food for refuelling, the birds were also confronted with strong westerly gales which swept across Europe (Fig. 4, panel 3 and 4 from top). These conditions made further migration almost impossible. Only swan #7275 managed to 'break out' by moving south from Estonia to Lithuania with tail wind on 20 October and to cross the Baltic Sea to S-Sweden on a still day a few days later. It spent a month in S-Sweden before continuing via W-Denmark to The Netherlands. All other satellite birds were held up in the Baltic area well into November and then slowly progressed to The Netherlands via Poland and Germany.

Due to long staging periods in the Baltic, arrival to the wintering grounds in The Netherlands was not until 7 November for the earliest bird (#7293) and 12 December for the last satellite bird

Fig. 4. Potential wind assistence (V_{tw}) per day in the Pechora Delta, the White Sea, Estonia/Finnish Gulf, Lithuania/Kaliningrad, and the Netherlands in autumn 1998. Upward and downward pointing arrows indicate the time of departure and arrival, respectively, of the individual satellite swans. Arrow 1 refers to swan #7274, arrow 2 to swan #7275, arrow 3 to swan #7292, arrow 4 to swan #7293 and arrow 5 refers to swan #7273 (compare Fig. 3b).

Table 4. Phenology of Bewick's Swan autumn arrivals in Lauwersmeer, The Netherlands. Accuracy of dates between brackets is ± 1 d. [a]defined as > 400 birds present on the lake; [b]date on which peak numbers were present on the lake; [c]date on which < 100 birds remained on the lake

Year	First arrival[a]	Peak arrival[b]	Departure[c]	Peak number
1990	(14 Oct)	15 Oct	(24 Oct)	1886
1991	23 Oct	23 Oct	(29 Oct)	2818
1992	4 Oct	18 Oct	28 Oct	874
1993	2 Oct	18 Oct	(16 Nov)	3500
1994	17 Oct	18 Oct	(27 Oct)	1999
1995	22 Oct	24 Oct	2 Nov	1600
1996	14 Oct	26 Oct	5 Nov	6922
1997	15 Oct	16 Oct	28 Oct	1908
1998	4 Oct	7 Oct	14 Oct	2228
1999	15 Oct	18 Oct	24 Oct	4000

(#7274). The total duration of autumn migration for the five tracked birds ranged between 41 and 78 d. However, based on departure dates from the Pechora Delta (usually around 25 September, own observations from 1992, 1993, 1996 and 1998 and S. Petrusjenko pers. comm.) and first arrival dates to The Netherlands (1990-1999), some birds apparently can cover the great circle distance of 3,200 km in a much shorter period. In 1992, 1993 and 1998 significant numbers of Bewick's Swans were already present in Lauwersmeer, The Netherlands in the first days of October, whereas peak arrivals usually take place in the second half of October (Table 4). In those years favourable tail winds occurred at each successive station along the route on succeeding days, enabling the birds to continue their south-westward migration (Fig. 5). Average maximum tail wind at the respective stations was 15.8, 15.7 and 13.1 km h^{-1} respectively in these early years, compared to an airspeed of 64 km h^{-1} calculated for satellite tracked Bewick's Swans (see Methods).

In contrast, in years in which the swans arrived at more normal dates in the third and fourth week of October, winds at at least one of the stations (Pechora, White Sea, Finnish Gulf or southern Baltic) continued to blow from south to westerly directions, probably preventing the swans to move further. These conditions were comparable to those which our satellite birds met in 1998. In 1990 and 1997, birds met headwinds in the Baltic area and were most likely stopped there. In 1991 and 1995, unfavourable winds persisted over the northern tundra range, and in 1994, 1995, 1996 and 1999 headwinds continued over NW-Russia in the early migratory season. In these years, swans should either have delayed their departure from the breeding grounds, or they should have stopped in the White Sea if they would minimise their flight costs.

When comparing the migratory performance on the stretch between stopover sites in the Baltic region and the breeding range in N-Russia, it becomes thus apparent that the swans make shorter leaps in spring than in autumn (t = -7.07, *df* = 5, *P* < 0.001) which is mainly caused by the fact that they skip the White Sea as a stop-over site in autumn. Speed of migration in spring was 29 and 38 km d^{-1} of the two birds that were tracked successfully to the breeding grounds, whereas in autumn this ranged from 44-72 km d^{1}. However, early arrivals to The Netherlands indicate that some flocks may complete their migratory journey of 3 200 km in a period as short as 8 d (25 September until 2 October), rendering a maximum speed of migration of about 400 km d^{-1} in autumn when Bewick's Swans are assisted by tailwinds.
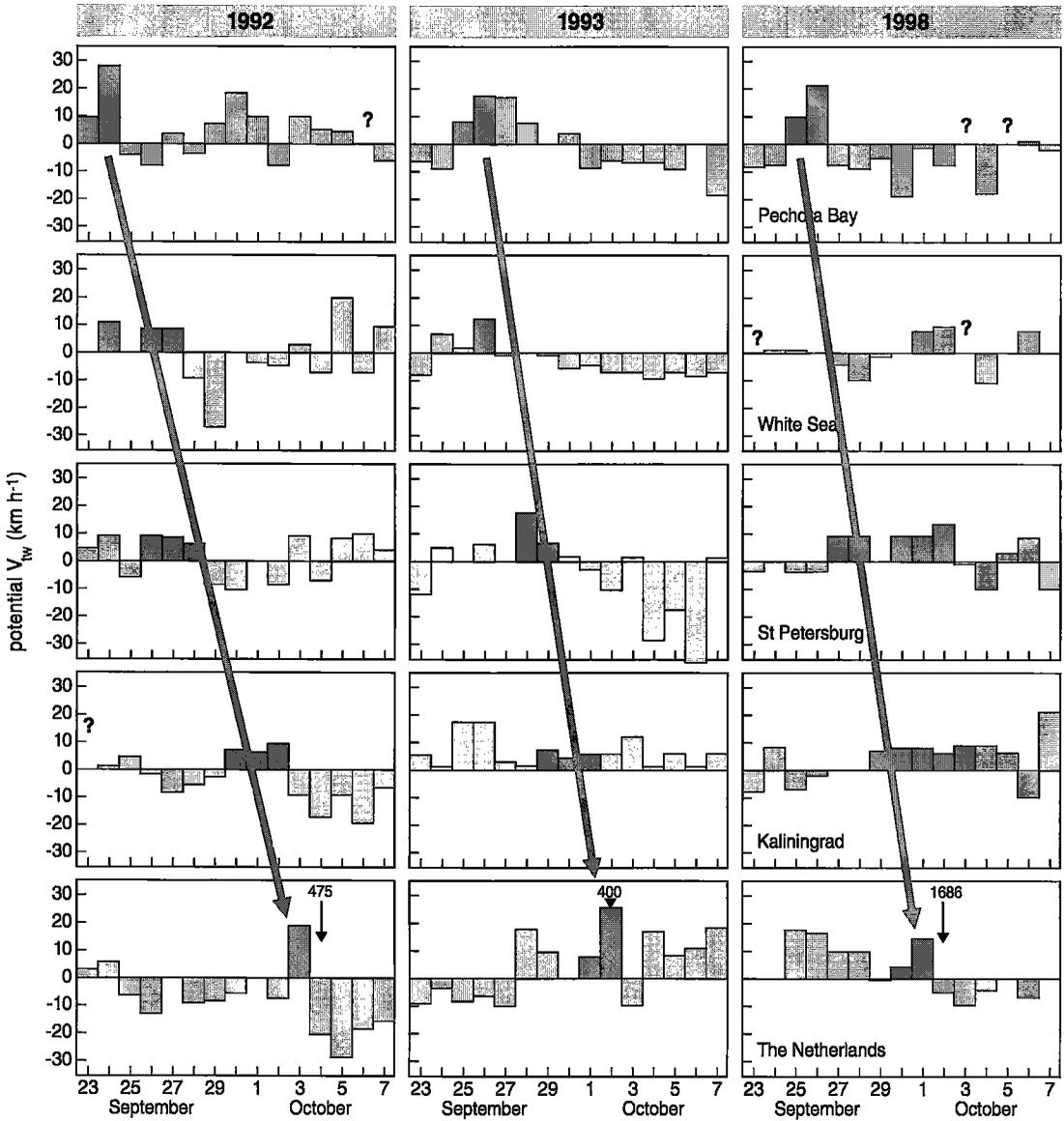
Fig. 5. Potential wind assistance (V_{tw}) at five weather stations along the migration route, between 23 September and 7 October in years when first arrivals in the Lauwersmeer (The Netherlands) were noted in early October (1992, 1993 and 1998). Dark grey bars indicate those days with favourable tailwinds, which would allow Bewick's Swans to migrate to the next station in time so that they could achieve early arrival in The Netherlands. First arrival date and number of swans are also indicated. In late years, continued head winds at one or more stations blocked further migration, see text.

Dynamic programming

For spring migration four decision matrices were calculated, one for each of the stopover sites, of fuel stores against time of year (Fig. 6). In each of the four panels areas of equal decision are indicated. Also indicated are combinations of fuel stores and time of year that do not enable the model swan to reach the breeding grounds at or after the optimal arrival date (i.e. 28 May or day 148). From inspection of the four panels it appears that the chronology of flights from the wintering to the breeding site is driven by the temporal variation in the availability of food (Fig. 2). The windows for departure to the next site(s) are narrow except for the departure from The Netherlands to Germany where food is available throughout the season and no depletion takes place. At other sites, food access is restricted by the seasonal presence of ice cover and by rapid depletion of food stocks due to swan consumption. A striking feature is also the large areas of 'no foraging' in the decision matrices and small areas of 'forage', at low fuel store levels and just prior to departure to the next site(s). This is a result of the fitness cost associated with carrying fuel stores (β in Appendix), which, however low, causes the swan to opt for low fuel stores when possible. Where fuel store levels approached zero, foraging was at the intensity just enough to maintain mass balance. When preparing for departure foraging intensity was maximal.

Forward simulations based on the decision matrix in Fig. 6 and starting on 16 February (day 47) in The Netherlands can roughly be divided into three different pathways depending on the initial fuel stores. Below a fuel store of 25% of lean body mass there is no reward. Above 50% the swans fly directly to Germany and between 25
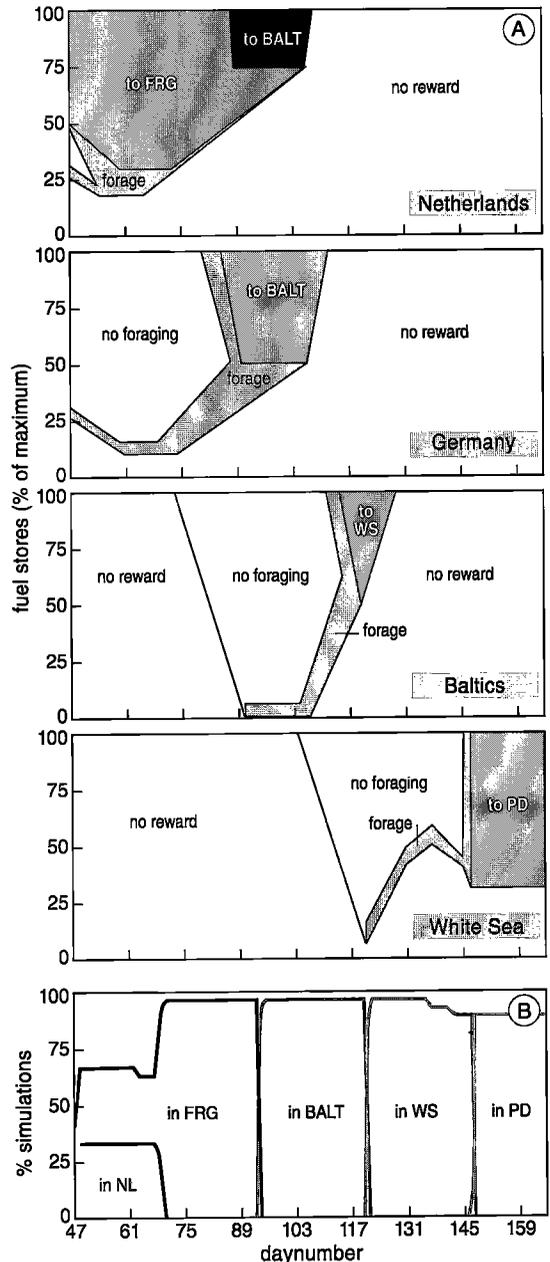
Fig. 6. (a) Decision matrices of Bewick's Swans for each major stopover site (The Netherlands NL, Germany FRG, Baltics BALT, and the White Sea WS) during spring migration to the breeding grounds in the Pechora Delta (PD), as determined by the backward calculation of the dynamic programming model. Swans with a combination of a fuel store and date within a certain section should either not forage, forage or fly to the next site, whereas swans with a combination within the section 'no reward' are not able to accomplish spring migration in time. (b) Time schedule of spring migration as determined by forward simulation, expressed as the percentage of simulations.

and 50% this departure is delayed until approximately day 69. From Germany onwards the pathways are identical: the swans depart as soon as food becomes available at the next site and maintain fuel stores as low as possible, typically arriving at the next site with close to depleted fuel stores. Thus departure from Germany with a fuel store of 52% takes place at day 95, departure from the Baltic with a fuel store of 60% takes place at day 122, and departure from White Sea with a fuel store of 38% takes place at day 148. Most importantly, the White Sea is predicted to be used in spring.

For autumn migration, which was modelled to start at 1 September (day 244), the decision matrix for the swans is straightforward (not depicted). The sooner the arrival at the wintering grounds, the higher the terminal fitness reward. Thus the swans always forage at maximum rate and fly to the next site(s) as soon as the fuel stores permit. In a forward simulation the total migration thus takes from 11 to 19 d for a bird with maximum and no fuel stores in the Pechora Delta at 1 September, respectively. Strikingly, irrespective of initial fuel load, with the foraging gain settings for the Pechora Delta depicted in Fig. 2e, the White Sea is never used as a staging site. This skipping is a result of the large foraging gain differences between the Pechora Delta and the White Sea. These foraging gain differences make it more profitable for the swans to overload in the Pechora Delta to enable a direct flight to the Baltic despite the higher flight costs associated with this overloading.

In order to investigate the sensitivity of this skipping behaviour for changes in foraging conditions in the White Sea and in the preceeding site, we varied the foraging gains at both sites without changing any of the other settings in the model (Fig. 7). The prediction of skipping appeared to be robust. Only with an isolated increase of *c.* 50% in the White Sea foraging gains or a decrease by *c.* 50% in the Pechora Delta foraging gains, stopover periods of >5 d are predicted. In contrast, the rate of depletion in the Baltic had to be more than halved before the swans were predicted to stop using the White Sea in spring (not shown).
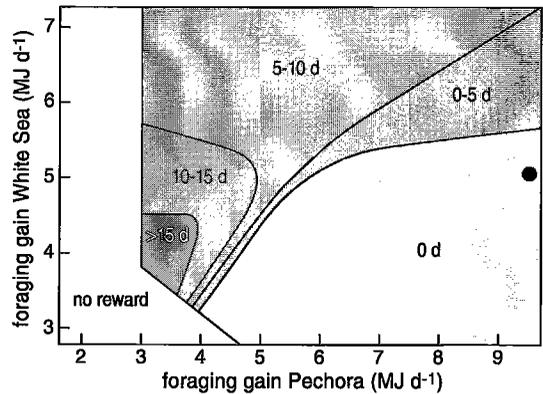
Fig. 7. The predicted length of autumn stopover in the White Sea for different combinations of foraging gains *G* in the White Sea and the preceding site in the Pechora Delta. The nominal combination (see Fig. 2) is indicated by the dot.

DISCUSSION

When bird movements are followed by tracking devices, the question always arises whether or not the birds' flight performance is influenced by the (external) transmitter. This can only be analysed under experimental conditions (cf. Holliday *et al.* 1988) or by comparing the flight performance of tracked birds with the migration of the population from which the experimental birds originate. In spring, swan #14551 made a stop-over of 20 d near Lake Ladoga in the vicinity of Petrozavodsk, an unusual site where only small numbers stage annually (V.B. Zimin, unpubl. data). From there it flew in the tail end of the migration wave, as was illustrated by its presence amongst the last 700 Bewick's Swans on 1 June 1993 in the White Sea (Nolet *et al.* 2001a). Swan #16109 arrived among the first swans in Estonia and departed from there across the Finnish Gulf simultaneously with the final large migration wave of Bewick's Swans on 17 May 1996 (Klaassen *et al.,* unpubl. data). This swan subsequently staged in the White Sea for 13 d, while most swans had left the area by the end of May (Nolet & Drent 1998). However, it arrived

well timed in the Pechora Delta one day after ice break-up on 4 June.

Four of the five autumn tracked swans left the Pechora Delta between 25 and 27 September 1998, when mass departure was observed there (Fig. 4; M. Klaassen, T. de Boer & H. Hangelbroek, unpubl. data). Most Bewick's Swans, including our satellite birds, arrived exceptionally early in the Baltics (V.A. Buzun, unpubl. data). In contrast, our satellite birds arrived rather late in The Netherlands (in November and December), but according to national census data that held for the majority of the population that year as well (Beekman 2000). We conclude that the tracked swans, with one exception, used only major stop-over sites known to be of importance for this flyway population of Bewick's Swans, and that their timing was in accordance with observations on migratory timing of the population as a whole. The only exception was swan #14551 that once made a stopover at a minor site in spring and was thereafter delayed by 2-3 weeks. Also swans tracked with transmitters in Japan and N-America do show normal migration patterns. Kanai *et al.* 1997 successfully tracked 8 Whooper Swans *Cygnus cygnus* from Japan to their Russian breeding grounds. Higuchi *et al.* 1991 tracked a female Bewick's Swan from Japan to the breeding grounds in NE-Siberia. This bird returned with offspring (!) to Japan in the next autumn. Petrie and co-workers have shown that the nominate Whistling Swan *Cygnus columbianus* can be tracked over even nearly two return trips between wintering and breeding range and these birds set remarkably good records in flight performance (S. Petrie & K. Wilcox, http://www.bsc-eoc.org/lpbo/swans/swans.html).

Observed and predicted migration patterns

The observed usage by swans of the White Sea stopover of *c.* 2-3 weeks during spring but not during autumn was also predicted by our dynamic programming model. The model indicates that the relative difference in quality between the site in the White Sea and the preceding site can determine whether swans stop in the White Sea or not.

Gudmundsson *et al.* (1991), using a simpler model with time minimisation as the birds' objective, already concluded that skipping was only expected when the previous site was of a better quality. Our virtual swan strived to maximise fitness, but it behaved as a time minimiser: in autumn, fitness is postulated to decline with arrival date, whereas in spring we postulated one possible arrival date, in fact the earliest date possible. An earlier arrival may be difficult due to ice cover along the migratory route and the high risk of having to bridge a period of adverse weather conditions shortly after arrival at the breeding grounds. Later arrival may lead to offspring mortality in autumn, in other words fitness declines with spring date. Time minimisation is further expected in spring because competition among breeders will conceivably lead to a highly synchronised arrival on the breeding grounds at the earliest date possible (Kokko 1999).

In autumn, the site preceding the White Sea is the Pechora Delta. Our data indicate that the Pechora Delta is of far better quality than the White Sea, with a daily foraging time nearly twice as long. Water level fluctuations due to the tide are much larger in the White Sea (0.3-1.2 m; Nolet & Drent 1998) than in the Pechora Delta (0.1-0.2 m; M. Klaassen, T. de Boer & H. Hangelbroek, unpubl. data). In the White Sea, pondweed only grows below mean low tide (Nolet & Drent 1998). Above mean low tide Bullrush *Scirpus lacustris* is the dominant plant species that is only sporadically eaten by swans, and the swans therefore hardly forage during high tide in the White Sea (Nolet *et al.* 2001a). In addition, depletion does probably not affect the swans' daily intake in the Pechora Delta where the pondweed beds are very large and the swans can constantly move to unexploited sites.

In spring, the site preceding the White Sea is located in the Baltic area. At that time of the year, ice cover prevents the exploitation of the large lakes, notably Lake Peipsi. The birds probably deplete the pondweed beds at least locally, and we expect that this negatively affects their intake rates. The difference in foraging gain between the

Baltic and the White Sea is already less than the difference between the Pechora Delta and the White Sea from the onset, but we suspect that it becomes gradually less due to depletion, to such an extent that skipping the White Sea is no longer optimal for the swans in spring. Our sensitivity analysis indicates that the predicted migration patterns are robust to plausible changes in foraging gain levels at the different stop-over sites.

Other potentially important factors are not considered in the model. In theory, larger fuel overloads are expected when there is a variance in fuel gain at the target site (Weber *et al.* 1998). Stochasticity in the onset of spring would also mean that the swans would benefit from carrying fuel stores to the breeding grounds in order to be able to sit and wait (Nolet *et al.* 2001b). Whether Bewick's Swans are capital or income breeders has not yet been resolved. In small arctic breeding birds, income breeding (i.e. the acquisition of resources for reproduction at the breeding grounds) seems to be the rule (Klaassen *et al.* 2001), but for large birds such as swans partial capital breeding (i.e. the usage of part of the body reserves as resources for reproduction) may be common (Meijer & Drent 1999; Klaassen *in press*). Mute Swans *Cygnus olor* are shown to be partial capital breeders by Ubels *et al.* (unpubl. data). If there is a premium on overloading on the penultimate site before the breeding grounds, the White Sea gains in importance because of its relative short distance to the breeding grounds (750 km). The distance from the Baltic to the Pechora Delta (1,850 km) is about equal to the maximum flight range of swans, which implies that swans skipping the White Sea will arrive on the breeding grounds nearly without reserves. Thus, any benefit from carrying fuel stores to the breeding grounds would lead to a more energy-selected and hopping-like migration in spring (Farmer & Wiens 1999). How relevant this is in Bewick's Swans remains to be assessed.

A visit to the island Mud'yug in early October 1996 revealed < 100 Bewick's Swans, mainly family parties, at an important spring site in the White Sea (Guba Sukhoye More; O. Langevoord,

unpubl. data). This observation can be seen as further evidence that Bewick's Swans generally skip the White Sea in autumn, but it also suggests that parents with cygnets at least partly behave differently from our satellite birds that were not accompanied by cygnets. Ely *et al.* (1997) tracked four female Tundra Swans that were returning from the breeding grounds in Alaska with cygnets, and recorded *c.* five short stops (<3 d) before the first main stopover period in central Alberta (3 200 km). Cygnets might not be able to sustain the long flights that adults manage, and the prime function of these short stops is believed to be resting and drinking rather than refuelling.

The ultimate skip

Average arrival dates in The Netherlands in autumn seem to be at deviance with the outcome of the dynamic programme, which predicts a much faster migration (11-19 d) than the 4-6 weeks from mass departure from the breeding grounds in the Pechora Delta (around 25 September) and mass arrival in The Netherlands (the last two weeks of October and the first week of November; Beekman *et al.* 1991). However, in 1992, 1993 and 1998 relatively large numbers of birds (400-1600) arrived at Lauwersmeer already in the first days of October (Table 4). These were mainly non-breeding or unsuccessfully breeding birds, which is in accordance with the observation that juveniles with their parents tend to arrive 2-4 weeks later than non-breeding and sub-adult birds (Beekman *et al.* 1991). Given a normal departure date from the Pechora, birds that arrive very early in The Netherlands may have covered the entire great circle distance of 3200 km within 5-10 d time. This means that, if we substract 3-4 d flying time (12 h d⁻¹), these birds had little or almost no possibility to replenish their fuel stores *en route*. Just how these early birds manage their peak performance remains to be elucidated. We have little information about these individuals, but a few birds marked in 1992 with neckcollars in the Pechora Delta have been sighted among early arriving birds in The Netherlands in the same year.

In contrast to the 'hopping' of an energy-

selected migratory bird, a time-selected migrant is expected to 'skip' and use only certain sites along the route. As a consequence the stopover durations are generally longer in time-selected migrants, and the probability that wind conditions will be favourable sometime during their stopover will therefore be greater. Moreover, the flights tend to be longer, and a tail wind advantage is therefore also of greater importance. Our data suggest that in some years favourable winds for onward flight are encountered at each subsequent station. As indicated in Table 1, the maximum flight distance (D_{max}) is 2023 km. However, if Bewick's Swans (which fly at an airspeed of 64 km h^{-1}) experience a tailwind assistance of 15 km h^{-1} (as they did in 1992, 1993 and 1998), this would increase their ground speed by almost 25%, allowing the birds to expand their maximum flight range. There is direct evidence from individually tracked Tundra Swans that distances of up to almost 3000 km can be covered non-stop under good wind conditions (S. Petrie, http://www.bsc-eoc.org/lpbo/swans/). Similarly extended non-stop flights are recorded annually for Pacific Brent Geese *Branta bernicla nigricans* whose departure is timed accurately by the passage of low-pressure areas and subsequent northwesterly winds, allowing the birds to cross the Pacific Ocean in a non-stop flight to Mexico (Dau 1992). These birds cover an estimated 4400 km great circle distance in moderate winds, while their D_{max} according to Pennycuick (1989) and Klaassen *et al.* (1999) is 3240 km in still air.

The mechanism

Although some of the satellite swans stopped in the White Sea for 1-2 d, we do not think that the birds sample the site before they decide to skip. Skipping of a stopover site implicitly means that the birds have to overload on the preceeding site, so the decision to skip has to be made long before the skip. It seems therefore more likely that the swans adopt the observed migration itinerary as a result of the poorer performance of swans using the White Sea in autumn. The mechanism through which poorer performance results in adjustment

of the migration can be individual experience, tradition or selection. Swans and geese are long-lived and operate in family units during large parts of the year (Cramp & Simmons 1977). These birds are widely regarded as traditional migrants with cultural inheritance of migration itineraries. However, Madsen (2001) recently provided empirical evidence for plasticity in spring stopover use in Pink-footed Geese *Anser brachyrhynchus*. His study nicely demonstrates that the birds adjust their migratory journey based on individual experience, with individuals being much more likely to change their itinerary from one year to the next when they had left the final stopover site in poor body condition than when they had left to the breeding grounds in good condition.

Cross-seasonal consequences of skipping behaviour

For Bewick's Swans, aquatic vegetation is the main food source during the migratory season, both in spring and in autumn. Tubers and rhizomes of pondweeds make up the main part of their diet, to a lesser extent followed by stoneworts (Characeae) and eelgrass *Zostera* spp. Since tubers of Fennel Pondweed are being formed in late summer or early autumn, just before the senescence and decay of above ground vegetation, they are a non-renewable food source, i.e. they are being formed only once a year and do not compensate for grazing by regrowth, as opposed to the leaves of most plants. Hence, the use of different stop-over sites by Bewick's Swans is likely to be connected, through biomass reduction, not only within but also between seasons.

The use of a given site in spring is unlikely to influence the use of the same site in autumn, since the tuber biomass in autumn is much more affected by conditions during the growth season than by the level of exploitation of tubers in the previous year (Jonzén *et al.* 2002; Nolet *et al.* unpubl. data). However, the use of a given site in autumn will invariably make a site less suitable for refuelling in the subsequent spring, because no tuber production will take place during winter. This must

then have consequences for birds visiting that particular site in terms of fuelling rates and hence migration speed. The result of visiting a site that was depleted in the previous autumn could be that birds will store less fuel or that they will be delayed in arriving at the breeding grounds. Both may lead to reduced reproductive success. When we apply this to the White Sea stop-over, which is the last stop-over before arrival to the breeding grounds, it can be envisaged that autumn exploitation in a certain year will lead to reduced breeding success of the entire population in the subsequent year. It is not unlikely that in autumns with persisting headwinds, the population will be forced to make a stop-over in the White Sea because they can not reach the Baltic in one flight under such wind conditions.

Testing the model

The dynamic programming model demonstrates that the skipping of the White Sea in autumn can be explained by differences in fuelling rates among sites. For Estonia, there is more direct evidence for differences in fuelling rates among sites. In spring, the ice-free coastal sites are exploited, but in autumn Bewick's Swans especially visit inland Lake Peipsi which is frozen over during spring migration. This means that coastal sites must be of less quality than the inland site in autumn, but it requires further determination of food stocks. However, this does not exclude alternative explanations. We see several ways forward from here. Firstly, parts of the dynamic programming model can be tested by comparing predicted and observed trends in behaviour and body mass at various stopover sites. The collection of body mass data is, however, hampered by the difficulty of trapping Bewick's Swans on water outside the moulting season. Secondly, modifications should be made to the dynamic programming model that add reality to it, testing whether these additions lead to better fits of predictions using maximum likelihood methods. Similarly, alternative models should be developed and their predictions compared with those of the best fitting dynamic programming model. Third-

ly, years with varying weather conditions (wind and precipitation) could be regarded as natural experiments. For instance, a multivariate analysis of reproductive success in relation to spring temperatures and autumn winds could be carried out as a next step. Fourthly, the migration of Tundra Swans in North America provides the opportunity for a comparative study.

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SAMENVATTING

Sommige trekvogels maken onderweg wel gebruik van een bepaalde pleisterplaats op weg naar het broedgebied, maar niet als ze naar hun wintergebied terugkeren. In theorie verwacht men dat een pleisterplaats alleen wordt overgeslagen door trekvogels die hun trek in een zo kort mogelijke tijd willen volbrengen en bovendien als het gebied waaruit ze vertrekken van een betere kwaliteit is dan de plaats die wordt overgeslagen. Wij leveren hier empirisch bewijs dat bij Kleine Zwanen *Cygnus bewickii* die bij ons doortrekken of overwinteren, het overslaan van een pleisterplaats onderweg inderdaad door kwaliteitsverschillen tussen de vertrek- en pleisterplaats wordt veroorzaakt. In het voor- en najaar werd van respectievelijk twee en vijf Kleine Zwanen die met satellietzenders waren uitgerust, de trek volledig geregistreerd. In de Witte Zee, waar in het voorjaar ongeveer twee weken werd gepleisterd, werd in het najaar niet of hoogstens enkele dagen gestopt. Een rekenmodel gebaseerd op berekende opvetsnelheden in de Petsjoradelta (nabij het broedgebied) en de Witte Zee, voorspelde dat de Kleine Zwanen de Witte Zee in het najaar moeten overslaan. Deze voorspelling bleek niet gevoelig voor aannemelijke veranderingen in opvetsnelheden. Het zoetwatergetijdengebied van de Witte Zee is een kwalitatief mindere pleisterplaats dan de Petsjoradelta, doordat tijdens hoogwater de velden van de ondergedoken waterplant schedefonteinkruid *Potamogeton pectinatus* onbereikbaar zijn voor de zwanen. Het rekenmodel voorspelde ook een snelle herfsttrek. Uit de aankomstdata in het overwinteringsgebied (het Lauwersmeer) bleek dat dit in slechts drie van de tien jaren voor een klein deel van de populatie werd waargenomen. In de andere jaren heersten er ongunstige winden op ten minste één van de opeenvolgende pleisterplaatsen, hetgeen waarschijnlijk een snelle doortrek heeft verhinderd.

APPENDIX

The dynamic programming equations

Weber *et al.* (1998) provide an elaborate account of the dynamic programming equations. Here only a brief description is provided, emphasizing the differences with the earlier models. Expected fitness at the final destination ($i = N$) is a function of date $K(t)$ plus the expected fitness from future breeding attempts B:

$$F(x,t,N) = K(t) + B$$

For spring migration, where N is the Pechora Delta (and $i = 1$ is The Netherlands):

$$K(t) \begin{cases} 0 & if \ t \neq 148 \\ 1 & if \ t = 148 \end{cases}$$

For autumn migration, where N is The Netherlands (and $i = 1$ is the Pechora Delta):

$$K(t) \begin{cases} 1 & if \ t = 244 \\ 1 - 1/121(t - 244) & if \ 244 < t < 365 \\ 0 & if \ t \geq 365 \end{cases}$$

Because reaching the breeding grounds is not a prerequisite for survival whereas reaching the wintering grounds is, B was set to 1 for spring migration and to 0 for autumn migration. Maintaining fuel stores incurs a fitness cost in terms of increased risks of predation, injury, and higher levels of energy expenditure (Witter & Cuthill 1993). We assumed that maintaining fuel stores x incurs only a small fitness cost β to the Bewick's Swans:

$$\beta(x) = m_\beta \frac{(x + uG(i,t) - E)^{a+1} - x^{a+1}}{(a+1)(uG(i,t) - E)}$$

where m_β was set to 10^{-8}, a was set to 2, G is the daily foraging gain, and E is the daily energy expenditure excluding foraging costs. If the Bewick's Swan decides to forage, is should forage with an intensity u that yields the maximum expected fitness at the final destination:

$$H_f(x,t,i) = \max_u[(1 - \beta(x))F(x + uG(i) - E, t+1, i)]$$

Alternative to foraging the Bewick's Swan can depart to one of the next sites depending on its fuel stores x and the distance D (km) to these sites. Its fuel stores upon arrival x_a at the next stopover were calculated using

$$x_a = (\frac{c^2}{(c - (c(1 - (1 + x/x_{max})^{-0.5}) - D))^2} - 1) \cdot x_{max}$$

where c is a flight range parameter which is calculated using

$$c = \frac{D_{max}}{1 - (1 + x_{max})^{-0.5}}$$

and D_{max} is the maximum flight range of the fully loaded Bewick's Swan from Table 1. If the Bewick's Swan decides to depart from site i, it should fly to $i+z$ (where $z \leq N$), yielding the maximum expected fitness at the final destination:

$$H_d(x,t,i) = \max_{i+z}[F(x_a, t + (\sum_{z=1}^{N-i} D_{i+z}/v), i + z)]$$

where v is migratory speed in km d^{-1} (Table 1). The optimal decision is the behavioural alternative yielding the highest future expected reproductive success:

$$F(x,t,i) = \max[H_f(x,t,i), H_d(x,t,i)]$$

For reasons of computation x, like t, must be a whole number. In the dynamic programme we therefore adopted a whole number unit of energy which was equivalent to 0.5 MJ.